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I. INTRODUCTORY REMARKS AND REVIEW OF THE LITERATURE

by A. P. Shcherbakov

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METABOLIC RATE AND LONGEVITY OF DROSOPHILA. I. INTRODUCTORY REMARKS AND REVIEW OF THE LITERATURE

A. P. Shcherbakov[1]

Summarizing the material regarding the duration of life and the metabolism in Drosophila melanogaster, the author concludes that all the existing material supports the theoretical concepts laid down by Rubner and developed further by E. Bauer.

Rubner's constant for normal (wild) Drosophila melanogaster equals approximately 8.7 mg of CO_2 per milligram of weight. This corresponds to 2.5×10^4 calories per 1 kilogram of weight, assuming RQ=0.85.

Rubner's constant may change with the change of the hereditary constitution of the fly. The mutation vestigial, the life of which is shorter and the metabolism is not higher but probably even lower than normal, may serve as an example.

From the fact that the constant proved the same at different temperatures (table IV) it follows that within the limits of a certain temperature range (physiologic limits), the longevity is in inverse proportion to the rate of the metabolism, other conditions being equal.

The difference in longevity between males and females is related to differences of the metabolism in inverse order. Rubner's constant therefore proves to be the same in both sexes. There are reasons to believe that this is only a single instance of a general rule which holds true for many organisms.

At present there is agreement among investigators of longevity that there /639* is an association between longevity and the rate of metabolism. The existence of this association was determined quite a long time ago by Rubner (ref. 1). While studying metabolism in different mammals he found that there was a difference in metabolic rate (per unit weight) which became larger the smaller the animal. However, when a calculation was made of the metabolism per unit weight of the animal during the entire life, a rather constant quantity was obtained (approximately 3.5×10^5 cal). From this Rubner concluded that longevity is determined by some activity factor which can be measured by metabolism and which, when exhausted, leads to death. This can be illustrated in the following manner:

*Numbers given in margin indicate pagination in original foreign text.

[1]Department of Biology of All-Union Institute of Experimental Medicine.

$$\text{basic } \frac{\text{metabolism}}{\text{weight}} \text{ (per day)} \times \text{longevity (in days)} = K.$$

where K is some constant.

Rubner's viewpoint was widely accepted by subsequent investigators. Thus Pearl et al (refs. 2 and 3) carried out a large series of experimental works on the study of longevity in Drosophila melanogaster and came to a conclusion close to that of Rubner. He assumes that the first factor in determining the longevity of some organism is the hereditary constitution which determines the total sum of activity which can be exhibited by the organism and the second is the metabolic rate (metabolism). In connection with this, by analyzing the effect of external conditions on longevity, Pearl reaches the conclusion that the action of these conditions is frequently achieved through a variation in the metabolic rate. Below we shall return to some of the works performed by the Pearl school.

The results of excellent work carried out by MacArthur and Baillie (ref. 4) on Daphnia magna are in complete agreement with the Rubner theory. The authors themselves are definitely in favor of the metabolic theory for longevity.

Recently E. S. Bauer (ref. 5) formulated the same law with a more definitive and theoretical basis. Proceeding from his general biological concepts, Bauer has shown that animal organisms must contain assimilation limits, i.e., a growth limit, and that the necessity for such a limit is determined by the specific characteristics of living matter. In each specific case this assimilation limit (measured in terms of the limiting weight achieved by an organism) is determined by the hereditary peculiarities of a specific organism. Longevity, according to Bauer, proves to be proportional to the assimilation limit and inversely proportional to the rate of vital activity. If we take the entire weight of an organism for expressing the assimilation limit and the magnitude of metabolism for the rate of vital activity, we obtain the following expression /640

$$\text{longevity (in days)} = K \frac{\text{weight}}{\text{metabolism per day}}.$$

It is easy to note that the relationship which Bauer obtained theoretically is identical to the one which Rubner established empirically on the basis of extensive data on mammals. The constant K in the Rubner equation corresponds to the proportionality factor in the Bauer expression and was called the "Rubner constant" by the latter. Thus the Rubner constant is the product of metabolic rate and the longevity computed for unit weight (for example, one kg), or in other words, this is the total quantity of energy which is converted by a unit mass of organism during its entire life.

As shown by Bauer, the magnitude of the constant is approximately the same for representatives of each systematic group (type) of animals but varies in a regular fashion when we go from one type to another. In general the constant is higher for higher organisms of a given type and beginning with a value of 6×10 cal for Coelenterata, it reaches a value of 3×10^5 cal in vertebrata (more

precisely, in mammals). We should note that the calculations were carried out for a very limited number of representatives and on the basis of data which are open to many objections. The dearth of exact information on the longevity and metabolism, particularly for invertebrata, makes it impossible at this time to make a broader check on the evolution side of the problem associated with the Rubner constant. One of the problems of the present series of works with Drosophila is precisely the clarification of the value of this constant for different forms of this fly.

Another problem which we are concerned with in this series of experiments consists of determining what happens to the Rubner constant for a given organism when we subject it to various reactions both during its period of development and during its adult life. Does this constant remain invariable? If it varies, how does it vary and under what conditions?

The selection of the Drosophila type flies as specimens was dictated by two considerations. In the first place this is a specimen for which the technique of laboratory breeding and housing in mass quantities has been developed to a high state of perfection, particularly as it applies to the determination of longevity. In the second place, Drosophila has a relatively short lifetime which is measured in terms of weeks and seldom in terms of months. This, of course, is an obvious advantage. The determination of metabolic rate in these flies does not pose great difficulties.

We should point out immediately that when we speak of longevity in the future we mean the average longevity determined by taking into account the natural extinction of a sufficiently large group of flies maintained under homogeneous conditions. The longevity of specific individuals varies over a wide range because flies already begin to die on the day following their hatching. The metabolic rate is determined by recording respiration. During this time the flies are in an active state and metabolism corresponds to active metabolism. Obviously it has nothing in common with basal metabolism which is usually studied in the physiology of higher animals. It should be borne in mind that the respiration of such active flies varies considerably among experiments and the spread in its value is 100 percent or more. This again makes it necessary to take the average quantity of a large number of determinations and to process the results statistically. The details of the methodology will be concerned specifically with the results of the experimental work.

A rather large number of works is devoted precisely to the longevity of Drosophila. The investigation of metabolism in these organisms has been carried out to a much lesser extent.

Let us consider first of all the works of Pearl and his coworkers (refs. /641
6, 7 and 8) on the average longevity of Drosophila melanogaster lines with different hereditary construction. A comparison of longevity under identical conditions for normal flies (the authors call them the wild type) and for flies with some mutation or with complex mutation has shown that all investigated mutations (if they are at all effective) lead to a decrease in longevity compared with normal lines. This reduction in longevity is different for different mutations and is particularly pronounced for the vestigial mutation (underdeveloped wings). Whereas the average longevity for normal lines according to

Pearl is equal to 45 days, the corresponding quantity for the vestigial line is approximately 20 days, i.e., it is reduced in half (t=25°C). The difference between normal and vestigial flies is manifested not only in the average longevity but in the nature of the extinction itself. The extinction curve for normal flies has a S-shaped form, i.e., at first the number of dying flies is small and the curve has a small slope; mortality increases with age and the curve drops more steeply; older flies are again characterized by retarded extinction and finally the curve again becomes flat and slowly approaches the axis. In the extinction curve for the vestigial flies the S-shape form is smoothed out and the entire curve approaches a straight line. Pearl crossbred normal and vestigial flies and in addition to the usual heredity picture associated with this mutation (disappearance in the first generation and occurrence in one-fourth individuals of the second) different longevity was also inherited. Of course these data do not indicate that special genes exist which determine longevity, but merely point out that the nature of the inherited constitution of vestigial flies also includes a decrease in the longevity of flies compared with the normal longevity.

The comparison of normal and vestigial flies has been the subject of a series of investigations. First of all Pearl (ref. 9) studied longevity during complete starvation and established that both types of flies live in an identical manner and the extinction curves are also similar. It turned out further that the extention curve of normal flies becomes very similar to the curve for vestigial flies when the maintenance conditions deteriorate. From these facts Pearl concluded that different longevity in normal flies and in vestigial flies is explained not by the hereditary differences and longevity but rather simply by the fact that the usual laboratory culture conditions (possibly nutrition) which are favorable for normal flies turn out to be unfavorable for vestigial flies. If the same beneficial conditions were created for the latter, the average longevity would be the same. However, it appears to us that it is difficult to explain a rather large difference in longevity of these two types of flies by the conditions of the culture. The behavior of vestigial flies under laboratory conditions does not indicate in any way that the usual conditions for the laboratory culture are unfavorable. It would be more natural to assume that the decrease in longevity is due to the general weakening of the inherited constitution. In this connection the experiments of Sekla (ref. 10) are of interest. This author investigated the effect of alcohol on the longevity of normal and vestigial flies under conditions of starvation. The flies were placed into test tubes without food. The cotton plug in each test tube had a shoot extending inside. This shoot was wetted with alcohol of different strengths and in control test tubes it was wetted with water. The results of these experiments are shown in table 1.

Alcohol in certain concentrations increases longevity compared with the case of complete starvation. Apparently the alcohol can be utilized to a certain degree by the flies as a nutrient. The most interesting feature is that even this insignificant improvement in nutrition conditions is enough to provide for a difference in the longevity of normal and vestigial flies. In the experiments conducted with water and with alcohol in low concentrations, the survival of both groups is the same; for high alcohol concentrations we can see that normal flies excel vestigial flies. This supports the viewpoint that under

TABLE 1. AVERAGE LONGEVITY OF DROSOPHILA MELANOGASTER DURING STARVATION (IN DAYS) ($t^{\circ}=25^{\circ}C$)

% alcohol	0.5	2	5	7.5	10	15	20	30
Normal flies	3.6	5.0	8.3	7.8	6.2	5.5	4.0	1.3
Vestigial	3.6	5.2	7.5	6.0	5.3	4.8	1.2	0.5

normal conditions of the culture, the shorter life of vestigial flies is due to/642 their hereditary characteristics and is not only the result of unfavorable conditions.

In addition to comparative data on the longevity of these two types, data are also available on the metabolic rate. Sekla (ref. 11) investigated the enzymatic activity of fly extracts ground with sand, and showed that extracts from vestigial flies have a smaller enzymatic activity than extracts from normal flies. This difference was observed with particular clarity in the case of the lipolytic enzyme when studying the breakdown of tributyrin. These data, although they are indirect, point to a lower rate of biological processes in the organism of vestigial flies. Sekla (ref. 12) also investigated the metabolic rate directly. It is true that his experiments were apparently quite few, but nevertheless it was clearly noted that the respiration of vestigial flies was weaker than that of normal flies. Thus we can conclude from all these data that longevity as well as metabolic rate and, consequently the product of these two quantities, will be substantially less in vestigial flies than in normal flies. There is no difference in the size of these two flies, and therefore the Rubner constant for vestigial flies will obviously be smaller than for normal flies.

A series of works has been devoted to the investigation of longevity and metabolism in Drosophila at various temperatures. The first of these is the rather old work of Loeb and Northrop (ref. 13) on the effect of food and temperature on all three stages of fly life: larval, pupal and imago. The works suffer from a series of shortcomings. The authors who were under the influence of the Mechnikov viewpoint deemed it necessary to work with sterile flies. At that time the possibility of obtaining sterile lines of Drosophila had already been shown in the works of Delecourt and Guyenot (ref. 14). To simplify their work Loeb and Norton used "glucose-agar" as a form of food. This is a rather complex substance consisting of meat bouillon, peptone, glucose and agar-agar but without any yeast. This food had the advantage that, because of the absence of yeast, larva did not develop in it while adult flies could subsist. As a result of this, frequent changes of food were not necessary and the maintenance of sterile conditions was made easy. By using only one small comparative series which was conducted at a very high temperature ($30^{\circ}C$), the authors concluded that the longevity of adult flies is the same regardless of whether their food contains yeast or not. However, the absence of yeast has a bad effect on flies and as subsequently shown by Alpatov (ref. 15) the longevity without yeast is almost half that of the longevity when yeast is used in the food. Also the fact that the existence of these sterile flies was not normal may be established from the progressive decrease in the longevity of subsequent generations. Thus in 1926, Northrop (Ref. 18) noted that for 195-205 generations of these sterile flies, there is a progressive decrease in longevity of

these cultures, particularly at low temperatures. The low longevity in the experiments of Loeb and Northrop can be clearly seen when they are compared with data obtained later by Pearl, who used a conventional neutral nutrient. The /643

data of Pearl are based on a very large amount of experimental work.[1]

A second shortcoming of the work is the rather small amount of material on individual series. With the very large variation in longevity it is necessary to have at least several hundred specimens to get an idea about the average quantity. In the works of Loeb and Northrop there is a case when the number of specimens in a series does not exceed 50. Also, there is no breakdown by sex.

In spite of these shortcomings the work still represents the only one which covers such a wide range of temperatures and all stages of the organism's life. The basic results are presented in table 2.

All of the flies which were used to determine the longevity of imago were developed at room temperature (18-20°C) and were distributed into different temperatures only after they emerged from the cocoons. At a temperature of 10°C the larva developed, although rather slowly, and formed cocoons. However

TABLE 2. THE LONGEVITY OF DROSOPHILA MELANOGASTER AT VARIOUS TEMPERATURES WITHOUT DIFFERENTIATION IN SEX

Temperature, °C	Longevity in days			
	Larval stage	Pupal stage	Adult flies	Total longevity
10	57.0	Cocoons perish	120.5	177.5
15	17.8	13.7	92.5	123.9
20	7.77	6.33	40.2	54.3
25	5.82	4.23	28.5	38.5
27.5	(4.15)	3.20	--	--
30	4.12	3.43	13.6	21.15

[1]In one of his books, Pearl (ref. 2) compares his data with the data of other investigators and in carrying out the comparison takes the average longevity obtained in his work including various mutations with decreased longevity. However, it seems to us that it would be more accurate to take this value for a normal line because it is doubtful that Loeb and Northrop were able to obtain such mutations as vestigial in their work.

The longevity of imago Drosophila melanogaster at 25° in days (without differentiation in sex) is as follows:

Loeb and Northrop..... 28.5
Pearl..... 45.0

cocoons perished at this temperature and adult flies did not emerge from them. Temperatures beyond the limits indicated in table 2 were also used and in this case it turned out that a temperature of 5°C is quite harmful for adult flies since their longevity is less than a week, whereas at 10°C it is equal to 120 days. The temperature of 30° is the upper limit and at higher temperatures the development of larva is retarded and there is a rapid decrease in the longevity of imago. Based on the data of Loeb and Northrop we may assume that the temperature range for the normal life of Drosophila is from 15°, or slightly lower, to 30°C. The temperature of 30°C is apparently too high since, at this temperature, the flies are sometimes barren. Within this range of temperature, longevity, both of individual stages and total longevity, varies inversely with the temperature: the higher the temperature, the shorter the longevity; the lower the temperature, the greater the longevity.

The basic purpose of the work carried out by Loeb and Northrop was to determine the temperature coefficients of longevity. /644 This aspect of the problem is of no particular interest to us at this time because we no longer feel that the mere determination of temperature coefficients and their comparison with coefficients for chemical reactions is the correct path for deciphering biological phenomena. This is particularly true because we must strain our imagination quite hard to acknowledge the existence of a definite coefficient considering that its value at different temperatures varies from 1.8 to 5.3 as established by Loeb and Northrop. Nevertheless we shall present the viewpoints of the authors concerning reasons which govern the longevity: "Observations on the temperature coefficient for longevity makes it possible for us to assume that this longevity is determined either by the production of material leading to aging and natural death or the destruction of material which normally prevents aging and natural death." Thus Loeb and Northrop, in concurrence with general ideas, had a tendency of considering the action of temperature on longevity as the acceleration and deceleration of some definite, although hypothetical, chemical reaction in the organism.

This simplified concept could not satisfy biologists who did not adhere to such physical and chemical concepts of the vital processes as Loeb and Northrop. Only a few years later Pearl (ref. 2) was inclined to explain the same data on the variation in the longevity of Drosophila with temperature changes by an increase in total metabolism at elevated temperatures and by its decrease at lower temperatures. This increase in metabolism has its external manifestation in high activity of the flies compared with their activity at lower temperatures. The effect of low temperatures on longevity is explained by a change in the rate of living under the action of temperature. An increase in temperature leads to the acceleration of life, to the accelerated depletion of the organism's energy budget and a decrease in longevity. The lowering of temperature works in the opposite direction. According to Pearl the total sum of energy which an organism can convert during its entire life is determined by heredity. This total amount of energy may be different for organisms with different hereditary constitution. The effect of external conditions (which of course are not of a lethal nature) leads to an increase or decrease in the vital processes and consequently to acceleration or deceleration of energy processes. Summarizing the viewpoints of Pearl we can state that according to him, heredity determines some total quantity of vital activity (measured by

metabolism), which the organism must exhibit in the course of its life and the environment determines the "rate" at which this quantity of vital activity is depleted, i.e., it determines the tempo of the organism's life. When the heredity factor is the same, longevity will be inversely proportional to the rate of vital activity (metabolism).

The effect of temperature on the longevity of Drosophila was also investigated in the work of Alpatov and Pearl (ref. 16). The authors experimented only with imago at three temperatures: 18, 25 and 28°C. Comparative data on the longevity of adult flies developed at different temperatures is of particular interest. The rounded-off values of average longevity are presented in table 3. There were approximately 500 flies of each sex in each of the experimental series.

In regard to the effect of temperature on the longevity of adult flies these data confirm the observations of Loeb and Northrop: the higher the temperature, the shorter is the average longevity.

Temperature during the development period also affects the subsequent longevity of adult flies. Flies which are developed at a low temperature (18°C) have a greater longevity than flies which are developed at a higher temperature (28°C), even in the case when they live under identical conditions /645
in their adult state. The differences are very pronounced during low temperature imago life and are smoothed out at high temperatures. We should bear in mind that flies which are developed at 18°C are larger than flies which have been developed at 28°C. The authors illustrate this by a series of examples, but unfortunately present no data on either the total dimensions of the entire body or the weight of these two groups of flies. Therefore, it is difficult to imagine the degree of difference. The flies developed at a high temperature (28°C) had a smaller longevity and at the same time were smaller than flies developed at a lower temperature (18°C). The question arises of whether these different fly sizes have the same Rubner constant or not? At the present time we do not have data for answering this question. It is generally known that the metabolic rate in organisms is usually inversely proportional to their size, i.e., the rate is greater in small organisms than it is in large ones. This is true both for mammals as well as for a series of other animals.

TABLE 3. LONGEVITY OF DROSOPHILA MELANOGASTER IMAGO IN DAYS AT DIFFERENT TEMPERATURES

Development temperature	18°C						28°C					
Temperature of imago life	18°		25°		28°		18°		25°		28°	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Average longevity for each sex	43.5	70.6	26.8	41.0	21.9	30.7	35.0	65.3	22.5	35.8	22.6	28.5
Average longevity for both sexes combined	57.05		33.9		26.3		50.15		29.15		25.55	

Recently the same relationship between size and metabolic rate was shown for crayfish of the Sorerod group by Shcherbakov (ref. 17). In all these cases there is discussion of differences in the size between various form or breeds which are due to heredity. On the other hand, in the case of large and small Drosophila obtained as a result of different temperature during development, we are speaking of phenotypic differences. Only special investigations will show whether in this case too, there is a difference in the metabolic rate. The possibility that in this case we are dealing with very complex relationships is seen from the results of another work by Alpatov (ref. 15). The author obtained flies from larvae which were fed normally and from larvae whose nourishment was inadequate. The normally fed larvae yielded flies of normal size while the undernourished larvae (those taken off their feed after 59 hours and given only agar-agar) produced flies of smaller size. Here there was the same relationship as in the preceding case but the difference in the size of flies was achieved by a different method. It turned out that the longevity of large flies and of small flies obtained by the undernourishment of larvae was the same. The average longevity (at 25°C) in the case of large flies was 49.1 days for females and 34.6 days for males; the corresponding longevities for small flies were 48.4 and 37.1 days. The differences are small and lie within the limits of errors. Thus a curious picture arises. The differences in the size of Drosophila either affect longevity or do not, depending on the method used to obtain this difference.

If the metabolic theory of longevity is valid and if, in particular, /646
Drosophila has a different life duration at different temperatures, because the same amount of energy is converted at a different rate, it follows that the metabolism of flies at different temperature must have the same value during the entire life. In other words, the product of metabolic rate and longevity at different temperatures (within the limits of physiological norms) must be the same.

A special verification of this proposition was carried out in one of the works of Northrop (ref. 18). By determining the production of CO_2 by Drosophila melanogaster during its entire life, including the period of larva development, Northrop found that, at different development temperatures, this production of CO_2 does not remain constant but is lower at a higher temperature than at a lower one. Thus one hundred flies during their entire life (with the exception of the cocoon period during which metabolism is very weak) at 15° produce 440 mg of CO_2, at 26° they produce 272 mg, at 30° they produce 246 mg while at room temperature (22-26°) they produce 411 mg of CO_2. From this Northrop concluded that longevity is not determined by the time necessary for the formation of a constant quantity of CO_2. In other words, if we assume that the formation of CO_2 is a measure of metabolic rate, then, when Drosophila is maintained at different temperatures the Rubner coefficient does not remain constant. However, the methods used in Northrop's experiments were crude and the number of experiments for each individual temperature was small (not more than 4) so that the

experimental results varied considerably and the average values determined from them are not very reliable. We shall now present the results of experiments carried out at 26°C. In four experiments the following values were obtained for CO_2 production in mg per hundred flies for their entire life: 189, 110, 260 and 210. With variations of this order the use of four experiments to obtain average values is quite insufficient. We should bear in mind that in Northrop's experiments the absolute value of CO_2 production by Drosophila during the entire life is very small. This is explained by the fact that the experiments were conducted using sterile lines of Drosophila developed by Loeb and Northrop. By this time (195-205th generation) the average longevity in these sterile lines had decreased substantially compared with the initial one which in general is normal for these flies.

The problem of longevity and metabolism at different temperatures was reinvestigated by Shcherbakov (ref. 9). The experiments were limited to the imaginal period and to two temperatures: 18 and 24°C. The liberation of CO_2 was taken into account for the nature of metabolic rate. There were twenty experiments in each series. Longevity was determined on the basis of a large amount of information. The basic results of this work are shown in table 4.

As we can see from table 4, longevity for both sexes was greater at 18° than at 24°. Judging by the liberation of CO_2, the metabolism, on the other hand, was greater at 24°. There is a quantitative relationship between the extension of life and the decrease in metabolic rate: longevity is extended by the same amount as the metabolic rate is decreased. This in particular, can be seen from the last column of the table. The total production of CO_2 during the entire life at two different temperatures is the same both for males and females. The computation of average errors for quantities presented in the table show that the variations from 8.2 to 9.2 mg in CO_2 during the entire life lie within the range of variability associated with the statistical nature of the material and have no real meaning. Therefore, we have all reason to assume that the conclusions of Northrop against the metabolic theory for the longevity of life are without basis and that there is indeed a characteristic value of vital activity for Drosophila (measured in terms of metabolism), which remains constant in spite of the fact that longevity at different temperatures is different. Or, in other words, natural death occurs after there is an apparent transformation of a definite quantity of energy and longevity depends on the rate of this process. /647

If we study in detail the values of longevity in tables 3 and 4 we can easily see that there is a regular difference between males and females. On the average, females live longer than males. In the experiments of Alpatov and Pearl (table 3), these differences between the sexes were extremely pronounced. Thus, for flies developed at 28° and living at 18°, the difference was 30 days (the females lived 65.3 days while the males lived 35.0 days. However, such

TABLE 4. THE TOTAL PRODUCTION OF CO_2 DURING THE ENTIRE LIFE OF DROSOPHILA MELANOGASTER

Sex	Temperature, °C	Longevity, days	Production of CO_2 in one mg for one mg of live weight per day	Total Production of CO_2 in mg per one mg of living weight during the entire life
Females	18	78.7	0.1107	8.7
Males	18	73.1	0.1118	8.2
Females	24	50.4	0.1731	8.7
Males	24	48.8	0.1877	9.2

large differences do not occur as a rule. Usually the average longevity of males is smaller than that of females by several percent. On the basis of a large amount of material, Pearl assumes that typical value for the longevity of Drosophila melanogaster is 45.8 days for males and 48.0 days for females at 25°C. In the first works on the longevity of Drosophila, results of an opposite nature were obtained. In the work of Loeb and Northrop mentioned above we find the statement that at 30° the males lived 15.7 days while the females lived 13.3 days. The same situation was observed in the experiments of Lutz (ref. 20). This discrepancy can be explained by the fact that the greater longevity of females is exhibited only under sufficiently favorable environmental conditions. As conditions deteriorate, longevity decreases and in this case females suffer more than males so that the differences between the sexes disappears and even becomes of an opposite nature. In earlier works on Drosophila the conditions of cultivation were far from optimum and this led, in the first place, to a general decreasing in longevity and in the second place, to the distortion of the normal relationship in the longevity of sexes.

The different longevity in females and male Drosophila is a particular case of a rather common phenomenon. It has been known for a long time that there is a difference in the average longevity of sexes in man. The longevity in women is somewhat greater (on the average by 6 percent) than of men. Large longevity was detected in the females of Daphnia by the experiments of MacArthur and Baillie (ref. 4). In this case the deterioration of conditions led to the disappearance of these differences. There are also indications of differences in longevity among sexes of diclinous plants. It is quite possible that we are dealing with a very general biological law.

Without going into a detailed discussion of the large amount of material on comparative longevity in sexes and into an attempt to explain this phenomena, we shall limit ourselves to only one question: what is the situation in regard to the Rubner constant in female and male Drosophila? Let us examine the data which have already been presented in table 4. In both cases, males lived somewhat shorter than females and at the same time their metabolic rate was higher. Of course we must bear in mind that although these differences are directed in the usual manner, their absolute value is very small and not completely reliable from the statistical point of view. Nevertheless if we take the total production of CO_2 during the entire life at two different temperatures then for females we have 8.7 and 8.7 mg CO_2 per 1 mg of living weight and for males we

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have 8.2 and 9.2 mg. Taking the average of these two figures we obtain an excellent coincidence: 8.7 mg for females and 8.7 mg for males. Thus, on the basis of these data we can state with a certain amount of conviction that the Rubner constant is the same for both sexes of Drosophila.

This same question is covered in two works of Gowen (ref. 21, 22). In the first work the author investigated the longevity of females, males, triploid females and intersexes of Drosophila melanogaster. The second work investigated the liberation of CO_2 by these same groups of flies. Table 5 presents the basic results of both works. Data on intersexes have been deliberately left out of the table because these flies are abnormal in many respects, with decreased longevity and it would be incorrect to compare them with the rest.

We can see from table 5 that normal and triploid females (triploid females are similar to normal females in all respects except that they are of larger size) have the same longevity and the same metabolic rate. In regard to the males, their longevity, as usual, is shorter than that of females. However, this is compensated by an increase in the metabolic rate and thus the total production of CO_2 during the entire life is the same for all three groups and is approximately 4.5 mg of CO_2. Consequently in this case the results are in favor of the proposition that the Rubner constant is the same for both sexes.

If we compare the total production of CO_2 during the entire life in tables 5 and 4, then it turns out that the quantities obtained by Gowen are almost half in value of those obtained in the analogous experiments of Shcherbakov (ref. 19). In part, this can be explained by the fact that Gowen determined longevity at 22°C and CO_2 liberation at 20°C, i.e., the measured metabolic rate was smaller than that of flies which were used to determine longevity. As a result of this there was a certain decrease in the product of these two quantities. Also in the experiments of Gowen the mean longevity was small which is particularly well illustrated by comparing data (table 6) obtained by various investigators.

It is possible that the decrease in longevity which follows from Gowen's work was due to hereditary factors inasmuch as he dealt with several unusual

TABLE 5. THE LONGEVITY AND LIBERATION OF CO_2 IN DROSOPHILA MELANOGASTER

Sex	Longevity in days at a temperature of 22°C	Liberation of CO_2 in mg per 1 mg of living weight during a 24-hour period at a temperature of 20°C	Total production of CO_2 in mg per 1 mg of living weight during the entire life
Triploid	33.1	0.136	4.5
Normal ♀	33.1	0.131	4.3
Normal ♂	28.9	0.167	4.8

TABLE 6. THE LONGEVITY OF DROSOPHILA MELANOGASTER

Author	Temperature, °C	Longevity in days	
		Females	Males
Pearl	25	48.0	45.8
Shcherbakov	24	50.4	48.8
Shcherbakov	18	78.7	73.1
Gowen	22	33.1	28.9

lines. The peculiarity of a line consists of the ability of females to form diploid eggs which are responsible for the origin of triploid females and of the intersexes.

The conclusions which we have reached concerning the Rubner constant for /649
different sexes of Drosophila are also confirmed for other organisms. As we have already pointed out above, the smaller longevity of males compared with females was discovered in Daphnia. MacArthur and Baillie (ref. 4) showed simultaneously that males have a higher metabolic rate and that the product of both quantities is the same in the different sexes. The same situation exists in man where shorter longevity of men is compensated by a more intense metabolic rate.

Conclusions

Summarizing what we have presented above concerning the longevity and metabolic rate in Drosophila melanogaster, we can state that all data at our disposal at this time are in agreement with the theoretical propositions presented by Rubner and developed subsequently by E. S. Bauer.

The value of the Rubner constant for normal (wild) Drosophila melanogaster is approximately equal to 8.7 mg CO_2, if we compute the metabolic rate per unit milligram of living weight. This corresponds to 2.5×10^4 cal for 1 kg of living weight, assuming that RQ=0.85.

The value of the Rubner constant may vary with the hereditary constitution of flies. An example of this is the vestigial mutation in which the longevity is less while the metabolic rate is not higher and most probably is lower than that of normal flies.

From the fact that the constant is the same at different temperatures (table 4) it follows that within the limits of the known temperature interval (physiological limits?) longevity is inversely proportional to the metabolic rate when all other conditions are equal.

The differences in the longevity of females and males are associated with the difference in the metabolic rate only when the latter is of an inverse order. Therefore, the Rubner constant turns out to be the same for both sexes.

There is substantial basis to assume that this is only a particular case of a law which is valid for a very large number of organisms.

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